

# AUSTRALIAN TERTIARY NEOLAMPADIDAE (ECHINOIDEA): A REVIEW AND DESCRIPTION OF TWO NEW SPECIES

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The age, stratigraphic horizon and distribution of each of the four known Australian Tertiary neolampadids and their associated echinoid fauna is discussed in light of recent discoveries. Two new taxa are described, the Late Eocene *Aphanopora? bassoris* sp. nov. and the Early Miocene *Actapericulum bicarinatum* gen. et sp. nov. Variations in the posterior profile and position of the periproct of *Pisolampas concinna* Philip 1963 and *Notolampas flosculus* Philip 1963 are also discussed and analysed.

With the discovery of *Aphanopora? bassoris* sp. nov., two distinct Cainozoic neolampadid lineages are postulated; one with a monobasal apical system and the other a tetrabasal apical system.

**Keywords:** Echinoidea, Neolampadidae, Tertiary, Australia, new taxa.

OF THE SEVEN monotypic genera previously assigned to the family Neolampadidae, only *Pisolampas* and *Notolampas* were known from the fossil record. Both of these have been found only in the Tertiary of southern Australia. The five extant genera have been recorded from the China Sea (*Anochanus*); the South Sulu Sea and Norfolk Island (*Aphanopora*); western Timor (*Aphanopora* and *Nannolampas*); eastern Florida to the West Indies and Bahamas, eastern Atlantic coast from the Bay of Biscay to Morocco and the Mediterranean (*Neolampas*); and South Africa (*Tropholampas*) (Mortensen 1948; Mooi 1990). Baker & Rowe (1990) also refer to ?*Aphanopora* from New Zealand and the Kermadec Islands.

Since the description of *Pisolampas* and *Notolampas* (Philip 1963), extensive collecting in South Australia and Victoria by R. J. and F. Foster in the 1970s, and more recently by F. C. and E. Holmes, has uncovered two further Tertiary neolampadid species. One is tentatively assigned to *Aphanopora* de Meijere and the other to a new genus.

In addition, neolampadid specimens from Kangaroo Island and Yorke Peninsula, South Australia, show that *Notolampas flosculus* and, to a lesser extent, *Pisolampas concinna* have a noticeable degree of variation in the posterior profile and the position of the periproct, features not discernible in the material available at the time of their original description.

## AGE, STRATIGRAPHY AND DISTRIBUTION

### *Late Eocene localities*

Neolampadids are known from three Late Eocene localities in southern Australia, each situated on the fringe of the St Vincent Basin, South Australia (Fig. 1, locs 1–3).

The description of *Pisolampas concinna* Philip 1963 was based on specimens from the Tortachilla Limestone, a Late Eocene (Aldingan, Bartonian–Priabonian) formation representing planktonic foraminiferal zones P14–15 (McGowran 1989). The Tortachilla Limestone, a yellow-brown, green and grey bioclastic limestone up to 2 m thick (Cooper 1979), crops out in the cliffs at the south end of Maslin Bay, about 40 km south of Adelaide (Fig. 1, loc. 1). The formation contains a rich echinoid fauna including, in addition to *Pisolampas*, the cassiduloids *Apatopygus vincentinus* (Tate 1891), *Australanthus longianus* (Gregory 1890), *Echinolampas posterocrassa posterocrassa* Gregory 1890, and *Enrhodia australiae* (Duncan 1877), forms which possibly share a common ancestry with neolampadoids. Because of the southerly dip of the strata, the Tortachilla Limestone does not crop out south of Blanche Point at the southern end of the Bay (Reynolds 1953; Cooper 1979). Many echinoids collected in the nineteenth and early twentieth centuries, now clearly attributable to the Tortachilla Limestone,

were referred to as originating from Aldinga and Port Willunga to the south of Blanche Point where the predominate Late Eocene to Middle Miocene Port Willunga Formation is exposed in the coastal cliffs and shore platform.

About 90 km southwest of Maslin Bay, low coastal cliffs of yellow-buff bioclastic Kingscote limestone occur for about 2 km southwest of the Kingscote jetty, Kangaroo Island (Fig. 1, loc. 2). This limestone, variously regarded in the past century as of Miocene or Eocene age, was assigned a Late Eocene age in the 1950s based on correlation with the Tortachilla Limestone (Glaessner 1953). The formation has since been shown to comprise three distinct lithological units separated by disconformities. Only the lowest unit correlates in part with the Tortachilla Limestone, with which it shares a similar rich Late Eocene echinoid fauna. The middle and upper units range in age from Latest Eocene to early Late Oligocene (Milnes et al. 1983). In the northeastern exposure of the lowest unit, which crops out between the foreshore swimming pool and the jetty at Kingscote, the oldest of the two new neolampadids, *Aphanopora? bassoris* sp. nov., is known to occur with *Pisolampas concinna* and a small undescribed species of *Monostychia*? The most abundant echinoids, *Australanthus longianus*, *Echinolampas postero-*

*crassa posterocrassa*, and *Fibularia gregata* Tate 1885, occur mainly in the southwestern exposure of the unit just north of Brownlow Beach. Unfortunately, the exact locality and horizon within the Kingscote Limestone from which the majority of specimens have been collected in the past has not been recorded.

Approximately 95 km northwest of Maslin Bay exposures of the Muloowurtie Formation in the vicinity of Harts Mine (13 km south of Ardrossan) and at nearby Muloowurtie Point, eastern Yorke Peninsula (Fig. 1, loc. 3), constitute the third of the Late Eocene localities at which neolampadids have been identified. Based on faunal evidence, the Muloowurtie Formation (redefined by Stuart 1970) correlates with the lower unit of the Kingscote Limestone and in part with the Tortachilla Limestone (Milnes et al. 1983). However, apart from Tate (1891) recording *Apatopygus vincentinus*, and an extensive collection of over 100 small specimens of *Pisolampas concinna*, little seems to be known about the total echinoid fauna of the Muloowurtie Formation, Stuart (1970) recognising only *Fibularia gregata*, *Salenidia tertiaria* (Tate 1877) and *Eupatagus* sp.

Although three other major Late Eocene marine formations in southern Australia correlate in part with the Tortachilla Limestone, the lower beds of

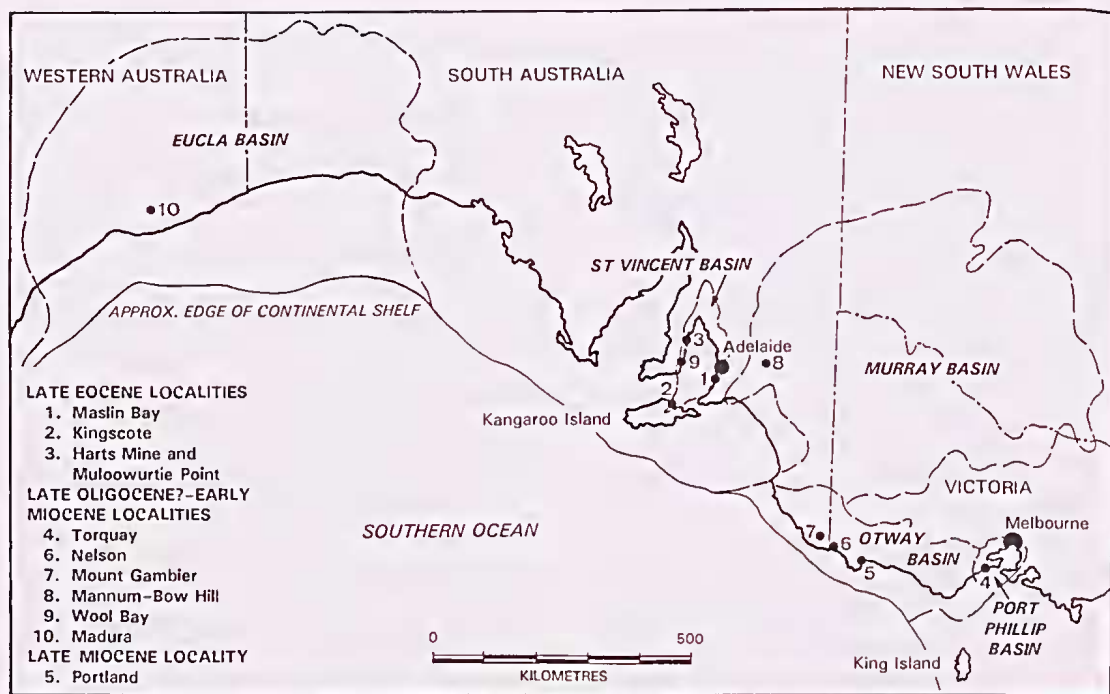


Fig. 1. Distribution of Late Eocene-Late Miocene fossil neolampadids in southern Australia.



the Buccleuch Group (Beds A of Ludbrook 1961), South Australia, and the Wilson Bluff Limestone and Nanarup Limestone, Western Australia, so far no neolampadids have been recorded from these formations.

#### *Latest Oligocene?–Early Miocene localities*

In contrast to the apparently restricted distribution of the two Late Eocene species, what are generally considered to be Early Miocene neolampadids have so far been found in the Port Phillip Basin, Victoria (Fig. 1, loc. 4); the Otway Basin, South Australia and Victoria (Fig. 1, locs 6–7); the Murray Basin, South Australia (Fig. 1, loc. 8); the St Vincent Basin, South Australia (Fig. 1, loc. 9); and the Eucla Basin, Western Australia (Fig. 1, loc. 10).

The Zeally Limestone Member of the Puebla Formation, a yellowish sandy bryozoan calcarenite with thin calcirudite interbeds, is exposed in coastal cliffs in the vicinity of Torquay, about 80 km south of Melbourne (Fig. 1, loc. 4). Planktonic foraminifers present in the Zeally Limestone indicate a Longfordian to ?Batesfordian (Burdigalian–Langhian) age, corresponding approximately to zones N6–8 (Abele 1988).

Associated with *Actapericulum bicarinatum* gen. et sp. nov. in a narrow band at the base of the low cliff between 200 m and 300 m southwest of Point Danger, are the echinoids *Lovenia* sp. and *Orbispala occultiformis* Irwin 1995. A single specimen of *A. bicarinatum* has also been found associated with the marsupiate echinoid *Paraspatangus* sp. about 2–3 m above high tide level at Point Danger.

The Early Oligocene to early Middle Miocene Gambier Limestone has also yielded neolampadids in the vicinity of the South Australia–Victoria border. *Notolampas flosculus* is known from the predominantly soft, white, chalky limestone exposed in a working quarry south of Mt Gambier (Fig. 1, loc. 7); in cliffs near Princess Margaret Rose Caves on the banks of the Glenelg River; and in an old quarry about 1.6 km north of Nelson, Victoria (Fig. 1, loc. 6). So far, *Actapericulum bicarinatum* gen. et sp. nov. has only been recorded from the latter locality. Based on the age of the Gambier Limestone cropping out in the vicinity of Nelson (Abele, pers. comm. in Kenley 1971), an Early Miocene (Longfordian to ?Batesfordian) age (between zones N5 and N8) seems likely.

The Early Miocene (Longfordian, Aquitanian–Burdigalian) Mannum Formation, exposed primarily in cliffs along the Murray River between Swan Reach and Mannum, South Australia (Fig. 1,

loc. 8), contains probably the richest echinoid fauna of any formation in Australia. However, as with Late Eocene material, little information exists on the exact location or stratigraphic horizon within the formation from which many early specimens were collected. In addition, the lack of published information on the stratigraphy of the Murray River cliffs makes it extremely difficult to determine the vertical distribution of any echinoid species. *Notolampas flosculus* Philip 1963 was described from specimens collected by Tate during the late nineteenth century from the general vicinity of Mannum. Ludbrook (1961) divided the type section of the Mannum Formation (Mannum pumping station) into lower and upper Members and listed the occurrence of various echinoids within each member; however, her identification of *Pygorhynchus vassali* Wright of Tate, 1891 (= *Notolampas flosculus*) in the lower of the two members is disputed by Philip (1963), who implies that Ludbrook's specimen is an *Echinolampas*. Although uncommon, specimens of *Notolampas flosculus* have been found over a fairly wide area; on the other hand, *Actapericulum* gen. nov. has so far been recorded from only one locality within the Mannum Formation, the cliffs adjacent to Coolcha Landing Recreational Reserve, 6.5 km west of Bow Hill. Specimens collected recently were found in a sparsely fossiliferous light yellow-brown bioclastic calcarenite about 20–23 m above mean river level near the top of the track leading down to the reserve. *Eupatagus rotundus* Dunean 1877, small *Fibularia gregata*, *Lovenia forbesii* (Tenison Woods 1862), *Ortholophus woodsi* (Laube 1869) and *Psephoaster klydonos* McNamara 1987, were found associated with the new genus.

In the St Vincent Basin, numerous specimens of *Notolampas flosculus* have been found in pale grey to dark yellowish grey bryozoan calcarenites and calcirudites of the Port Willunga Formation (= Port Vincent Formation in Stuart 1970) exposed in coastal cliffs between Stansbury and Edithburgh on the east side of Yorke Peninsula, South Australia (Fig. 1, loc. 9). As there is no stratigraphic break between the Oligocene and Miocene in the Port Willunga Formation no precise age can be given for the occurrence of *Notolampas*. However, based on the probable occurrence of the Oligocene–Miocene boundary in the cliffs (and adjacent quarry) at Klein Point, north of Wool Bay (Stuart 1970), and the gentle southerly dip of the strata to the south of Wool Bay, a latest Oligocene?–Early Miocene (Longfordian) age seems likely. Out of the 35 specimens of *Notolampas* from Yorke Peninsula, examined in the Museum of Victoria collections, 25 were found

between 0.75 and 2.25 km south of the jetty at Wool Bay where they are associated with *Echinolampas morgani* Cotteau 1890, a typical Early Miocene species.

At Madura (Fig. 1, loc. 10), in the Western Australian part of the Eucla Basin, specimens of *Notolampas* have been found in the yellowish porous bryozoan calcarenites and granule calcirudites of the Early Miocene (Longfordian) Abrakurrie Limestone which disconformably overlies the Late Eocene Wilson Bluff Limestone (Hocking 1990). Philip (1970) identified *Pisolampas* sp. nov. in a field sample taken from just above the base of the Abrakurrie Limestone at Abrakurrie Cave (approx. 140 km east of Madura), and suggested that 'in the Abrakurrie Cave at least, the Wilson Bluff Limestone may pass conformably up into the Abrakurrie Limestone without any hiatus'. A search through Abrakurrie Limestone fossils held by the Geological Survey of Western Australia failed to locate this specimen, so the occurrence of *Pisolampas* in this formation cannot be confirmed.

#### *Late Miocene locality*

Recently, a single partially encrusted 20 mm long neolampadid almost certainly assignable to *Notolampas* has been found by Mr C. Ah Yee, associated with specimens of *Lovenia bagheerae* Irwin 1994 about 2 m above the base of the foreshore cliffs below the lighthouse at Portland, south-western Victoria (Fig. 1, loc. 5). This section of the Port Campbell Limestone represents the upper part of zone N16 and the basal part of zone N17 (Singleton et al. 1976), making this specimen Mitchellian (Tortonian) in age and the youngest representative of *Notolampas*.

### MATERIAL AND METHODS

The primary material on which this study is based is housed in the invertebrate palaeontological collection of the Museum of Victoria (specimen numbers prefixed NMV). Some secondary material used in statistical analysis is currently held in the author's private collection. Measurements were made with a dial calliper to an accuracy of 0.1 mm. Parameters are expressed as a percentage of test length (%TL) followed by the mean, the standard deviation (SD) and the number of specimens measured (N). In specimens of *Pisolampas concinna* and *Notolampas flosculus* variations in the height and width of the periproct are expressed as a percentage of test height (%TH) and test width (%TW) respectively.

### SYSTEMATIC PALAEOONTOLOGY

Order NEOLAMPADOIDA Philip, 1963

Suborder NEOLAMPADINA Philip, 1963

Family NEOLAMPADIDAE Lambert, 1918

Genus *Aphanopora* de Meijere, 1903

*Type species.* *Aphanopora echinobrissoides* de Meijere, 1903 (extant) from the Sawu Sea (Timor) and South Sulu Sea (Philippines); original designation.

*Remarks.* In his brief description of *Aphanopora echinobrissoides*, de Meijere (1903) did not separate generic and specific characteristics, although he later (de Meijere 1904) gave a clear generic diagnosis which is, with the possible exception of the reference to the periproctal plates, applicable to the fossil species described herein. Unfortunately de Meijere's diagnosis lacks any information on the apical plate structure, which presumably was not visible on either of his two specimens. Because of this lack of information on the type species, the Late Eocene species *A. ? bassoris*, which is clearly tetrabasal, is only tentatively placed in *Aphanopora*.

Mortensen (1948), although noting that he had not seen these specimens, also included a generic diagnosis. This contains characteristics of the type species not used by de Meijere, namely: paired depressions in the adoral ambulacral plates; details of the primary spines and pedicellariae; and the lack of phyllodes or bourrelets. The latter reference contradicts de Meijere's statement that the floscelle is poorly developed. An abbreviated version of Mortensen's generic diagnosis is used by Durham & Wagner (1966). Two additional specimens of *Aphanopora echinobrissoides* from 240 km north of Norfolk Island were briefly described and figured by McKnight (1968), but no further information is added to de Meijere's (1904) description of the genus.

*Aphanopora ? bassoris* sp. nov.

Figs 2A, B, 3A-M, 51-L

*Etymology.* Latin *bassus*, meaning 'deep', and *oris*, meaning 'mouth', referring to the deeply sunken peristome. Noun in apposition.

*Holotype.* NMV P140922 from the Late Eocene (Aldingan, Bartonian?-Priabonian) Kingscote Limestone (lower bed), Kingscote, Kangaroo Island, South Australia; collected by L. McNeil, April 1990.

*Paratypes.* NMV P73675-P73682, P133072, P133073 and P140923 from the same member/horizon and locality as the holotype.



*Other material.* A single specimen in the private collection of Enid Holmes (EH 23), from the same member/horizon and locality as the holotype.

*Diagnosis.* Small moderately inflated ovoid neolampadids with centrally depressed adoral surface and greatest width and height posterior to centre. Apical system central, tetrabasal, with two gonopores. Ambulacra narrow, simple, non petaloid with a row of extremely small single pores in each half ambulacrum adorally. Phyllodes absent, bourrelets poorly developed. Peristome transversely oval, anterior of centre. Periproct supramarginal, longitudinally oval at the upper end of an elongated anal groove. Test evenly but not closely covered with small primary tubercles.

*Description.* Test small, specimens ranging from 9.7 to 11.0 mm in length (mean = 10.2 mm, SD = 0.4, N = 12), ovoid in outline at the ambitus with slight to moderately truncated posterior margin. Maximum width 87–93% TL (mean = 90.3%, SD = 2.1, N = 12) occurs 52–63% TL from anterior ambitus (mean = 57.6%, SD = 2.8, N = 12). Aboral surface moderately inflated, in lateral profile curving fairly steeply upwards from a well rounded anterior margin to reach a maximum height of 48–59% TL (mean = 53.3%, SD = 3.0, N = 12) between 50–64% TL from anterior ambitus (mean = 56.0%, SD = 4.2, N = 12) and, posterior of the apex, obliquely truncated to steeply curved. Viewed transversely, the aboral surface is evenly convex to obliquely truncated bilaterally and the adoral surface flat to mildly concave. The ambitus,

anteriorly and laterally, is situated at about 20% of the test height (TH) above the lowest point, rising to about 27% TH posteriorly. Both aboral and adoral surfaces of test have small randomly placed sunken primary tubercles generally uniform in size but slightly larger towards the ambitus.

Apical system basically central, ranging between 44–54% TL from anterior ambitus to centre line of gonopores (mean = 47.8%, SD = 3.1, N = 10), tetrabasal (ethmophract), anterior genital plates 2 and 3 being smaller than the adjoining posterior genital plates 1 and 4 which contain the two gonopores. Distinct dimorphism is present, female gonopores being markedly larger than those of male specimens of similar size. Ocular plates small; II, III, and IV in contact with apical disk, 1 and V separated from disk by first row of posterior interambulacral plates. Up to 5 or 6 hydropores may be present anterior to the two gonopores in genital plate 2.

Ambulacra simple and relatively narrow, with the majority of plates containing a single primary tubercle. The presence of single pores in each column adapically cannot be determined although they occur adorally.

Interambulacra broad, each zone between three and four times width of adjoining ambulacral zones at the ambitus, with individual plates very much larger adorally than adapically. Anterior interambulacra 2 and 3 narrower than others.

Floscelle not developed, although several specimens show signs of incipient bourrelets. While phyllodes do not appear to be present, in two

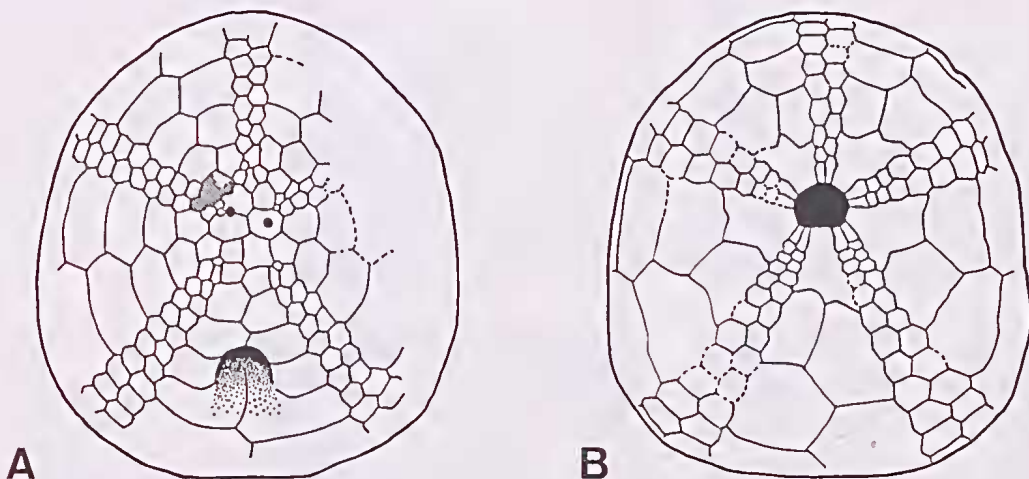
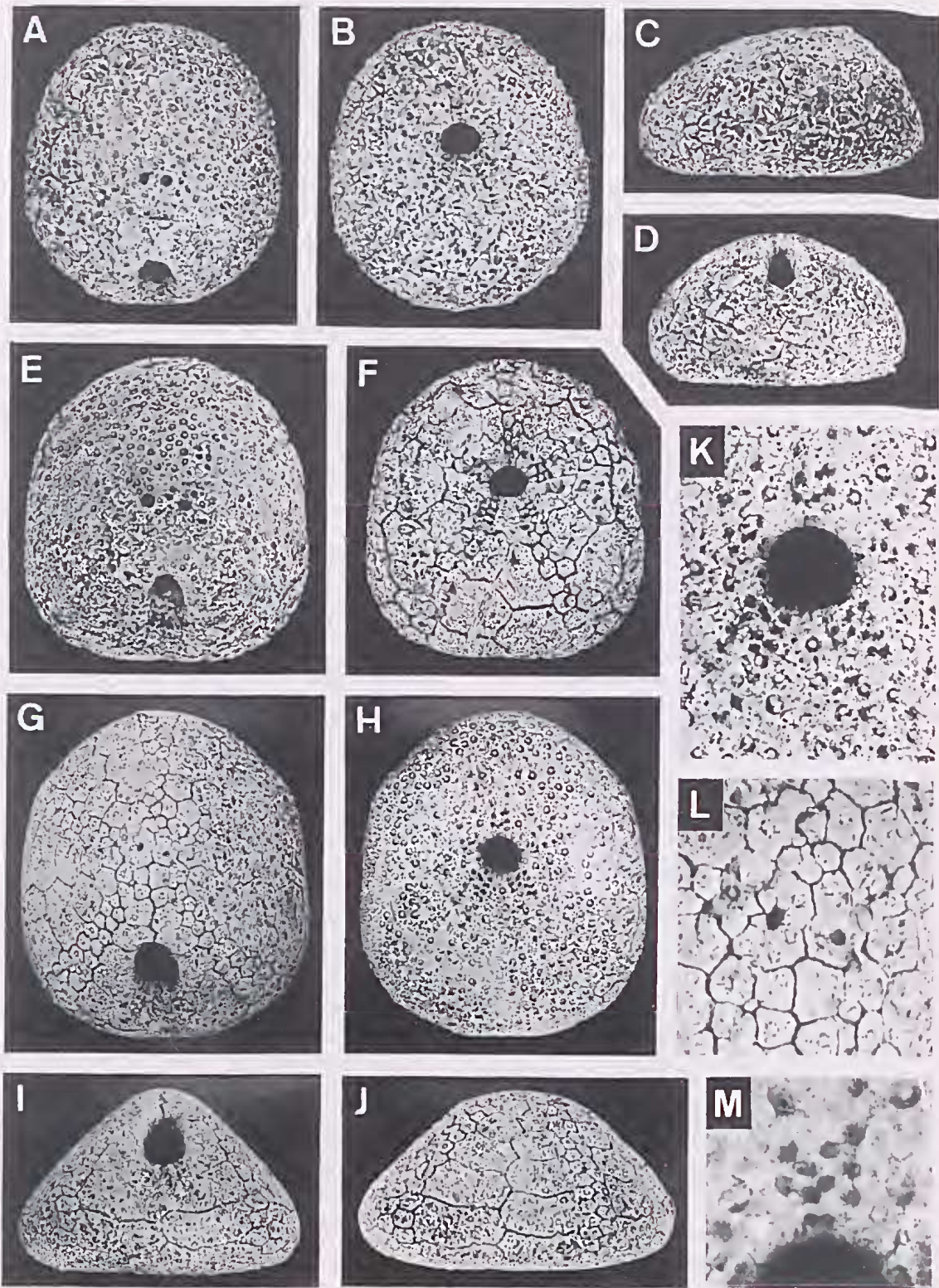


Fig. 2. *Aphanopora? bassoris* sp. nov. A, apical plating of paratype, NMV P140923 (♂). B, adoral plating of paratype, NMV P133073 (♀). Both  $\times 5.5$ .





specimens there is evidence of pairs of very small, staggered, transversely elongated pits in ambulacral plates adjacent to the peristome (Fig. 3K, M). Buccal pores are also visible in one specimen.

Peristome anterior, transversely elliptical to sub-pentagonal, (width about 13% TL, length about 10.5% TL) at base of a deep well in shallow adoral depression situated 38–43% TL to centre from anterior ambitus (mean = 41.4%, SD = 1.3, N = 12).

Periproct supramarginal but not visible from above, small, subcircular to oval, deeper than wide, positioned nearly vertically beyond the anterior end of a moderately deep anal recess extending almost to the posterior margin. Anterior edge of anal groove 22–34% TL from posterior ambitus (mean = 28.7%, SD = 4.0, N = 12).

**Remarks.** De Meijere (1903, 1904) based his description of the extant type species partly on morphological features rarely, if ever, preserved in fossil specimens. While many of these features are well described and figured, details of the test shape are vague and can only be interpreted from very small sketches of the adoral surface and the lateral profile (de Meijere 1904: pl. 19, figs 372, 373) and one equally small photograph showing an oblique view of the adapical surface (pl. 6, fig. 79). In addition no information is given about the apical system plate structure, the location of the oculars or sexual dimorphism. A considerable number of features of *A.? bassoris*, appear to be almost identical to those of *A. echinobrissoides*, such as the ambulacral plating, tuberculation, shape and position of the peristome and periproct, and the occurrence of paired pits in the ambulacra adjacent to the peristome. However, when compared with de Meijere's illustrations and dimensions of *A. echinobrissoides*, *A.? bassoris* is very much smaller in size, proportionately higher and wider, lacks the apparent swelling below the ambitus in interambulacra 1 and 4 and lacks the concave 'pinched' lateral profile of the adapical and adoral surfaces posterior to the highest point.

McKnight's (1968) photographs of the adapical and adoral surfaces of one of the more recently collected specimens of *A. echinobrissoides* also

show a considerable similarity with *A.? bassoris* in size and general appearance, although both the peristome and anal groove of the former appear to be very much wider. Unfortunately McKnight does not include either a posterior or lateral view of *A. echinobrissoides* and illustrations in Mooi (1990) appear to be only interpretations of McKnight's photographs.

Amongst other neolampadids, *A.? bassoris* appears to be most closely related to the extant species *Nannolampas tenera* (de Meijere 1903), both possessing tetrabasal apical systems with two gonopores. *N. tenera* is easily distinguished from *A.? bassoris* by its strongly truncated posterior and circular marginal periproct. The lack of a marsupium in female specimens distinguishes *A.? bassoris* from the poorly described *Anochanus sinensis* Grube 1868.

### Genus *Pisolampas* Philip, 1963

**Type species.** *Pisolampas concinna* Philip, 1963 from the Late Eocene (Aldingan) Tortachilla Limestone of Maslin Bay, South Australia; original designation.

**Diagnosis.** See Philip (1963: 718).

### *Pisolampas concinna* Philip, 1963

Figs 4, 5A–H

*Pisolampas concinna* Philip 1963: 719, pl. 106, figs 1–10, pl. 107, fig. 11, text-fig. 1a–c. — Durham & Wagner 1966: U630, fig. 516, 1a–d.

**Remarks.** Comparison of specimens of *Pisolampas concinna* from the Kingscote Limestone, Kangaroo Island (Fig. 1, loc. 2), and the Muloo-wurtie Formation, Yorke Peninsula (Fig. 1, loc. 3), with specimens from the type locality (Fig. 1, loc. 1), show that the species exhibits a noticeable variation in the height of the periproct above the base of the test (Fig. 5A–H). There are two fairly distinct groups; the periproct of specimens from the Kingscote Limestone being lower on the posterior face (marginal to slightly supramarginal) when compared with those from the Tortachilla Limestone and the Muloo-wurtie Formation, all of which are clearly supramarginal

**Fig. 3.** *Aphanopora? bassoris* sp. nov. All figures  $\times 4.5$  unless otherwise stated. A–D, holotype NMV P140922 ( $\phi$ ), adapical, adoral, lateral and posterior views. E, F, NMV P133073 ( $\phi$ ), adapical and adoral views. G–L, NMV P140923 ( $\sigma$ ), adapical, adoral, posterior and lateral views; detail of peristomal area ( $\times 12$ ); and detail of apical system ( $\times 12$ ). M, NMV P73678 ( $\sigma$ ), detail of paired pits and buccal pores in ambulacrum III adjacent peristome ( $\times 15$ ). All specimens from the Late Eocene Kingscote Limestone, Kangaroo Island, South Australia.

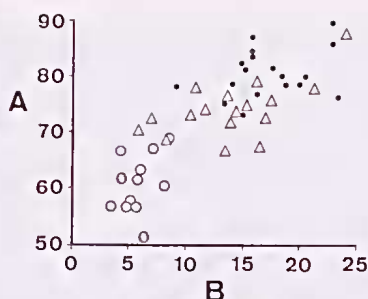


Fig. 4. Bivariate plot of periproet position in Late Eocene specimens of *Pisolampas concinna* Philip from the Kingseote Limestone (○), Muloowurtie Formation (●), and Tortachilla Limestone (△). A (vertical scale), height to top of periproet opening as % test height. B (horizontal scale), anterior end of anal recess to posterior ambitus as % test length.

(Fig. 4). While this variation is distinct in the specimens so far collected and examined, apart from a gradual increase in the length of the test of specimens from the Muloowurtie Formation (range 5.0–10.5 mm, mean = 6.87 mm,  $N=35$ ) through those from the Tortachilla Limestone (range 6.6–12.1 mm, mean = 9.61 mm,  $N=22$ ) to those from the Kingseote Limestone (range 9.8–15.4 mm, mean = 12.65 mm,  $N=13$ ), there are no other major differences. Even the test length to height, width, position of apex, widest point and peristome ratios remain virtually constant in specimens from the three formations. This evidence suggests that specimens from all three localities belong to a single, somewhat variable species rather than distinct subspecies.

### Genus *Actaperciculum* nov.

**Etymology.** Latin *acta*, meaning 'headland', and *periculum*, meaning 'danger', referring to the locality Point Danger, Victoria, from which the majority of specimens originate. Gender neuter.

**Type and only known species.** *Actaperciculum bicarinatum* sp. nov.

**Diagnosis.** Small, mildly inflated, subcircular to ovoid neolampadids, with concave adoral surface and greatest width and height posterior to centre. Apical system monobasal, with four gonopores and small to moderately sized pierced oculars. Ambulacra with row of single pores in each column from phyllode to ocular. Elongated supramarginal periproet at anterior end of long deep anal groove extending to posterior margin. Peristome

longitudinally orientated, anterior of centre with well developed floscelle having clearly defined bourrelets and expanded phyllodes.

**Remarks.** The combination of four gonopores and an elongated supramarginal periproet easily distinguishes this genus from other neolampadids. *Tropholampas* H. L. Clark 1923, the only other neolampadid genus to have four gonopores, is very much smaller and has a highly inflated test, a marginal periproet and, in females, an adapical marsupium. Two other neolampadid genera are recorded as having elongated supramarginal periproets, *Anochanus* Grube 1868 and *Aphanopora* de Meijere 1903; the former, although known only from a single specimen, can be distinguished from *Actaperciculum* gen. nov. by the presence of an adapical marsupium; and the latter can be distinguished by the presence of only two gonopores, a transversely orientated peristome, rudimentary bourrelets and the lack of phyllodes.

The presence of a well developed floscelle in *Actaperciculum* could be taken as evidence of a closer affinity with the cassiduloids rather than with other genera of neolampadids. However, the similarity between *Actaperciculum* and the Late Eocene *Pisolampas*, the Early Miocene *Notolampas*, and the extant *Neolampas* in other characters (see Discussion on p. 126) necessitate placement in the Neolampadidae.

### *Actaperciculum bicarinatum* sp. nov.

Figures 6A–M, 8I–L

**Etymology.** Latin *bi*, meaning 'two', and *carinatus*, meaning 'keeled', referring to the pronounced adoral swelling of interambulacra 1 and 4.

**Holotype.** NMV P140924 from the late Early Miocene (Longfordian–?Batesfordian, Burdigalian–Langhian) Zeally Limestone Member, Puebla Formation, Point Danger, Torquay, Victoria; collected E. Holmes, September 1994.

**Paratypes.** NMV P73689–P73703, P73710–P73724, P140925, P140926 and P140929 from the same member/horizon and locality as the holotype; NMV P73683 from the Early Miocene? of the Early Oligocene–early Middle Miocene Gambier Limestone, Mt Gambier, South Australia; NMV P73684–P73688 from the Early Miocene (Longfordian–?Batesfordian) Gambier Limestone, near Nelson, Victoria; and NMV P73704–P73709 from the Early Miocene (Longfordian) Mannum Formation, near Bow Hill, South Australia.

**Other material.** Two specimens (FCH1 and FCH2) from the Early Miocene (Longfordian) Mannum Formation, near Bow Hill, South Australia, in the author's private collection.

**Diagnosis.** As for genus.



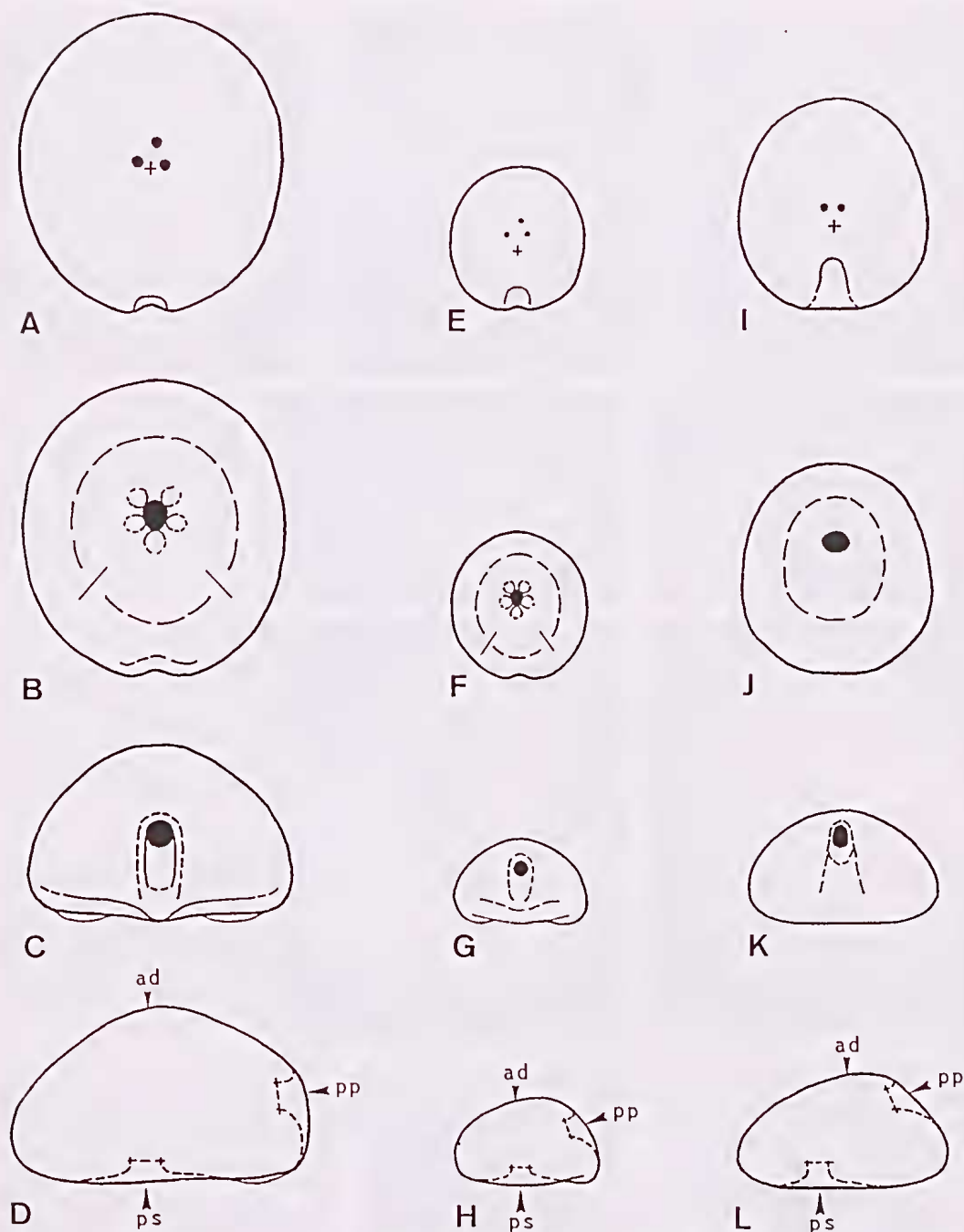
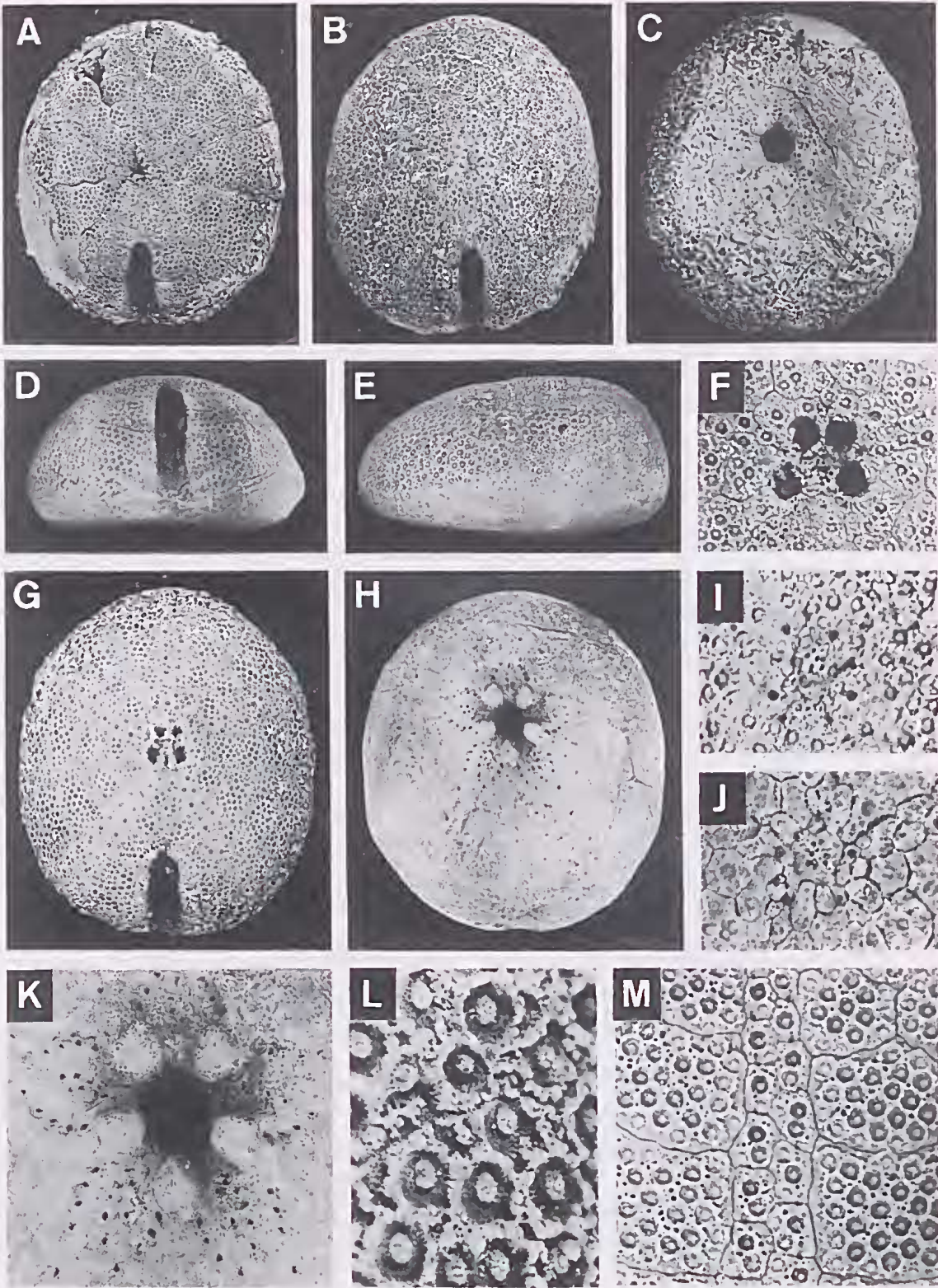


Fig. 5. Comparative drawings of Late Eocene neolampadids in adapical (A, E, I), adoral (B, F, J), posterior (C, G, K) and lateral (D, H, L) views;  $\times 3$ . *Pisolampas concinna* Philip, A–C, NMV P140927 (♀) from the Kingscote Limestone, Kingscote, Kangaroo Island, South Australia; and E–H, NMV P73839 (?) from the Muloowurtie Formation, Muloowurtie Point, Yorke Peninsula, South Australia. *Aphanopora? bassoris* sp. nov., I–L, NMV P140922 (♀) from the Kingscote Limestone, Kingscote, Kangaroo Island, South Australia. Broken lines and arrows on lateral views indicate centre of apical disk (ad), periproctal recess (pp) and peristomal recess (ps).





**Description.** Test small, specimens ranging from 9.6 to 16.4 mm in length (mean = 13.5 mm, SD = 1.9, N = 31), subcircular to ovoid in outline at the ambitus with slightly truncated posterior margin indented at base of anal groove. Maximum width 80–93% TL (mean 87.2%, SD = 2.7, N = 27) occurs 50–57% TL from anterior ambitus (mean = 53.4%, SD = 1.7, N = 27). Aboral surface mildly inflated, gently curving upwards from a well rounded anterior margin to reach a maximum height of 42–53% TL (mean = 48.6%, SD = 3.4, N = 17) between 51–59% TL from anterior ambitus (mean = 54.9%, SD = 2.8, N = 15). Posterior of the apex the aboral surface is more steeply curved, some specimens tending to be obliquely truncated in the vicinity of the anal groove. Transversely the aboral surface is evenly convex. Adoral surface flat or mildly depressed centrally with interambulacra 1 and 4 swollen below the ambitus to display a concave profile viewed anteriorly or posteriorly and a convex profile viewed laterally. The ambitus, anteriorly and laterally, is situated at about 30% of the test height (TH) above the lowest point (base of swollen interambulacra) rising to about 38% TH posteriorly. Both aboral and adoral surfaces of test covered with small closely spaced sunken crenulate and perforate primary tubercles (Fig. 6L).

Apical system slightly anterior of centre, 43–50% TL from anterior ambitus to centre (mean = 47.0%, SD = 2.1, N = 22), monobasal with four variably situated gonopores, anterior pair closer together than posterior pair. In the few male specimens where the plate structure can be observed, the four gonopores occur within the interambulacra on or close to the interradial sutures but generally in contact with the apical disk. However, in at least two specimens, two or more of the gonopores have migrated to the distal suture of one or other of the first pair of interambulacral plates and in another even into the second pair. Distinct dimorphism is present, female gonopores being very much larger than those of male specimens of similar size. Ocular plates variable in size, perforated by a single pore and generally in contact with the genital disk. Hydropores centrally

located, usually between seven and ten in number but as many as fifteen may be present.

Ambulacra simple adapically, narrow, with row of small single pores in each column extending from phyllode to ocular, each pore situated adradially on, or immediately adjacent to the transverse suture between adjoining plates (Fig. 6M). Primary tubercles on ambulacral plates increase progressively in number from one in plates close to oculars to about six in plates at ambitus of large specimens.

Interambulacra broad, each zone between four and five times width of adjoining ambulacral zones at ambitus. Anterior interambulacra 2 and 3 slightly narrower than others, lateral interambulacra 1 and 4 swollen adorally.

Floscelle well developed with a gently rounded and moderately inflated granulated bourrelet in each interambulacrum, bulging slightly into the well of the peristome. Phyllodes variably expanded, but of even length, with large single pores in two series in each half ambulacrum, four or five pores in each outer series and usually one or two in each inner series although up to four may be present. The occurrence of occluded plates in the ambulacra can not be determined from available material. Buccal pores are present.

Peristome anterior, longitudinally subpentagonal to oval (length about 11% TL, width about 9% TL), moderately sunken and situated 39–43% TL to centre from anterior ambitus (mean = 41.1%, SD = 1.4, N = 20).

Periproct supramarginal and clearly visible from above, narrow, elongate, up to twice as long as wide, lying obliquely to the horizontal at the anterior end of a long deep anal groove extending to the posterior margin. Anterior end of anal groove 25–36% TL from outer edge of posterior indentation (mean = 28.9%, SD = 2.88, N = 27).

**Remarks.** Statistical analysis is based solely on the measurement of specimens from Point Danger, Torquay, Victoria (Fig. 1, loc. 4). Analyses of specimens from the Nelson-Mount Gambier area (Fig. 1, locs 6, 7) and from the Murray River near Bow Hill (Fig. 1, loc. 8) shows that both groups

Fig. 6. *Actapericulum bicarinatum* gen. et sp. nov. All figures  $\times 3.2$  unless otherwise stated. A, L, M, NMV P140925 (? $\sigma$ ), adapical view; detail of primary tubercles ( $\times 30$ ); detail of adapical interambulacrum ( $\times 12$ ). B, C, I, holotype NMV P140924 ( $\sigma$ ), adapical and adoral views; detail of apical system ( $\times 12$ ). D, E, NMV P73685 ( $\sigma$ ), posterior and lateral views. F, NMV P140929 ( $\phi$ ), detail of apical system ( $\times 10$ ). G, NMV P73691 ( $\phi$ ), adapical view. H, K, NMV P73689 (?), adoral view; detail of floscelle ( $\times 8$ ). J, NMV P140926 ( $\sigma$ ) detail of apical system plate structure ( $\times 12$ ). NMV P73685 from the Early Miocene Gambier Limestone, Nelson, Victoria; all others from the Early Miocene Zeally Limestone Member, Puebla Formation, Torquay, Victoria.

fall well within the parameters set down for the new species. The only notable variations are the shorter anal groove in specimens from Nelson Mount Gambier; and the much smaller test size of those from near Bow Hill, the smallest being only 7.6 mm long.

Apart from the presence of an additional gonopore and the position of the periproct with its consequent effect on the posterior shape of the test, *A. bicarinatum* is similar to *Notolampas flosculus*, particularly in the detail of ambulaera, peristome and tuberculation. However, the floscelle in *A. bicarinatum* is more pronounced than in *N. flosculus*.

In the past, several authors have noted a strong superficial resemblance between some neolampadid genera and the cassiduloid *Apatopygus recens* (Edwards 1836). This resemblance is particularly noticeable in small specimens of *Actapericulum bicarinatum* from the Mannum Formation in South Australia, where a species of *Apatopygus* also occurs. However, the latter is easily distinguishable from *A. bicarinatum* by the presence of narrow open petals, pairs of pores, a transverse peristome, and the lack of a discernible floscelle.

#### Genus *Notolampas* Philip, 1963

*Type species. Notolampas flosculus* Philip, 1963 from the Early Miocene (Longfordian, Aquitanian-Burdigalian) Mannum Formation, near Mannum, South Australia; original designation.

*Diagnosis.* See Philip (1963: 719)

#### *Notolampas flosculus* Philip, 1963

Figs 7, 8A-H

*Pygorhynchus Vassali* Wright.—Tate 1891: 275

non *Pygorhynchus Vassali* Wright.—Duncan 1877: 41, 67.—Duncan 1887: 420.—H. L. Clark 1946: 358.—Ludbrook 1961: 44

*Notolampas flosculus* Philip 1963: 720, pl. 107, figs 1-10, text-fig. 2a, b.—Durham & Wagner 1966: U630, fig. 516, 2a-d.—Sadler, Pledge & Morris 1983: 27.

*Remarks.* Examination and measurement of 47 specimens of *Notolampas flosculus*, in the Museum of Victoria collections, indicate a great deal of variation in the position of the periproct, variation not evident in the seven specimens on which the original description was based. These more recently collected specimens, ranging in length from 8.0 mm to 19.0 mm, are from the Gambier Limestone near Mount Gambier, South Australia and near Nelson, Victoria; the Mannum Formation near Mannum, South Australia; and the Port Willunga

Formation near Stansbury, Yorke Peninsula, South Australia (Fig. 1, locs 6-9). The variation shows a continuous gradation between very distinct end members and is not related to the different collection localities. At one end of the range is a specimen similar to the type material but with interambulacrum 5 markedly swollen on the adoral surface anterior to the submarginal periproct (Fig. 8A-D), whereas at the other end there are two specimens in which the periproct is supra-marginal, being very high on the scnituncated posterior surface above the ambitus but still obscured from above by a projecting lip in interambulacrum 5 (Fig. 8E-H). Intermediate forms have the periproct at varying heights above the lowest point of the test and the angle of the posterior laterally truncated adoral surface ranging between 40° and 85° to the horizontal. In all cases the recessed opening of the periproct is not visible from above, and, except in two or three specimens, it is not visible from the posterior. The overall variability of these features (Fig. 7) precludes recognition of two distinct subspecies.

The only significant differences between the specimens from the three localities are: the greater test height of specimens from the Port Willunga Formation (mean = 53.7% TL) and Mannum Formation (mean = 52.5% TL) compared to those from the Gambier Limestone (mean = 44.1% TL); and the much narrower width of the periproct in specimens from the Mannum Formation (mean = 12.6% TW) than in those from the Port Willunga

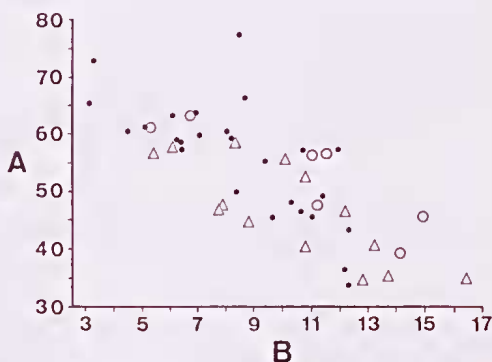


Fig. 7. Bivariate plot of periproct position in Early Miocene specimens of *Notolampas flosculus* Philip from the Gambier Limestone (○), Mannum Formation (△) and Port Willunga Formation (●). A (vertical scale), height to underside of lip or beak overhanging periproct as % test height. B (horizontal scale), anterior end of anal recess to posterior ambitus as % test length.



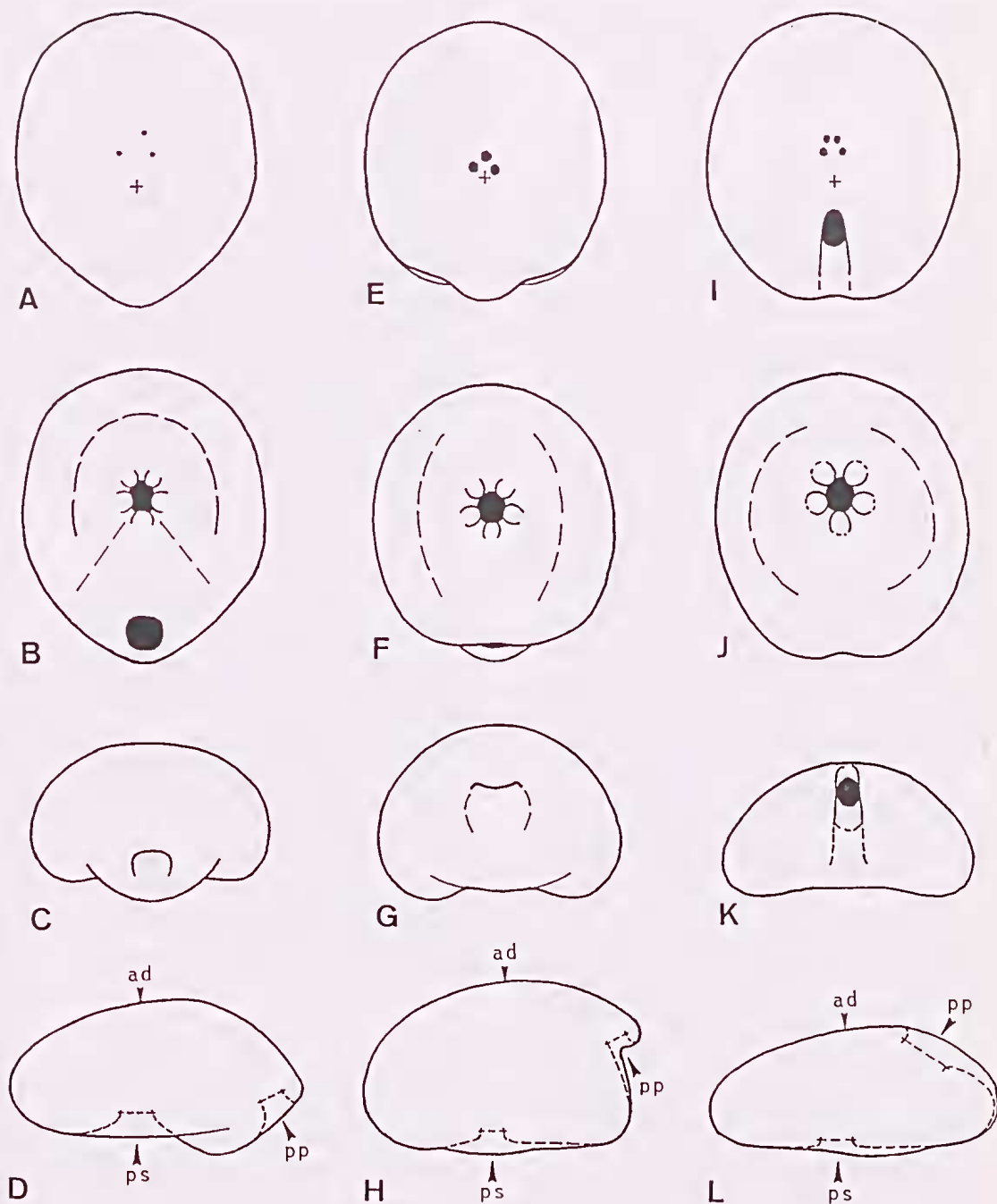


Fig. 8. Comparative drawings of Late Oligocene?–Early Miocene neolampadids in adapical (A, E, I), adoral (B, F, J), posterior (C, G, K) and lateral (D, H, L) views,  $\times 3$ . *Notolampas flosculus* Philip, A–D, NMV P140928 ( $\sigma$ ) from the Mannum Formation, Younghusband, South Australia; and E–H, NMV P145090 ( $\varphi$ ) from the Port Willunga Formation, Stansbury, Yorke Peninsula, South Australia. *Actapericulum bicarinatum* gen. et sp. nov., I–L, NMV P73701 ( $\varphi$ ) from the Zeally Limestone Member, Puebla Formation, Point Danger, Torquay, Victoria. Broken lines and arrows on lateral views indicate centre of apical disk (ad), periproctal recess (pp) and peristomal recess (ps).

Formation (mean = 17.0% TW) and the Gambier Limestone (mean = 17.8% TW). These features by themselves are also not considered sufficient to justify the recognition of subspecies.

## DISCUSSION

The discovery of the non-marsupiate Late Eocene *Aphanopora? bassoris* almost certainly refutes the suggestion (Mortensen 1948; Durham and Wagner 1966; McKnight 1968; Mooi 1990) that the two specimens on which the extant genus *Aphanopora* is based are males of the extant genus *Anochanus*, the only known specimen of which is marsupiate.

This Late Eocene discovery also clearly shows that at least two distinct neolampadid lineages have existed for most, if not the whole of the Cainozoic Era. One lineage, with a monobasal apical system, moderately well developed floscelle, and ambulacral pores extending from the peristome to the apical system, is represented by the Late Eocene *Pisolampas*, the Early Miocene *Actapericulum* and *Notolampas*, and the extant *Neolampas* (A. Agassiz 1869). The other lineage, with a tetrabasal apical system, no discernible floscelle, and aboral ambulacral pores atrophied or possibly absent, is represented by the Late Eocene *Aphanopora? bassoris*, the extant *Nannolampas* (based on Mortensen's 1948 description and illustration), and probably the extant *Aphanopora echinobrissoides* (the apical system plate structure of this latter species is undescribed).

The two extant marsupiate genera *Anochanus* and *Tropholampas* cannot easily be placed in either of the above lineages, the former because of the lack of any detailed description or illustration (although Grube [1868] stated that the rows of single ambulacral pores extend from the peristome to the apical system), and the latter because of its monobasal apical system but lack of any discernible floscelle. However, *Tropholampas* is similar in one respect to some, but not all, specimens of *Pisolampas concinna* in having the ambulacral columns and oculars separated from the monobasal genital plate by the interambulacra.

Stefanini (1913), Mortensen (1948), Philip (1963), and Durham & Wagner (1966) have each in turn postulated a cassiduloid ancestry for the neolampadids. Durham & Wagner (1966), in raising the group to ordinal status, stated that the lack of petals adapically and the nature of the ambulacral pores suggest that the neolampadids are secondarily specialised from a cassiduloid ancestry or were derived from an ancestor with poorly developed bourrelets and petals. In a

study based only on extant genera, Mooi (1990) recognised only the familial standing of the neolampadids, placing them in the Cassiduloida pending phylogenetic revision of the order's living taxa.

The discovery of the two additional fossil species, and the obvious separation of genera into at least two lineages, strongly reinforces the view of Mortensen (1948) that the Neolampadidae may not be a natural family. Further, Suter (1994) in a cladistic analysis of living cassiduloids, including neolampadids and three representative clypeasteroids, noted that phylogenies based on 'taphonomically robust' characters likely to be preserved in fossils, fail to support neolampadid monophyly. Suter also noted that, in all analyses carried out, the neolampadids form the sister group of the clypeasteroids, with most of the analyses placing the cassidulid genus *Studeria* (a species of which occurs in the Early Miocene of Australia) as the sister taxon to the neolampadid clypeasteroid clade.

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